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Marsenina pax, a new species of Velutinidae Gray, 1840 (Gastropoda: Velutinoidea) from the Yellow Sea, China

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ABSTRACT

During an investigation of the intertidal zone of Taiping Bay in Qingdao, China, three shelled gastropods were sampled. Morphological observations of these specimens suggest that they represent an undescribed species that belongs to genus *Marsenina* Gray, 1850. In the present study, we describe and illustrate it as *Marsenina pax* new species. This species can be clearly separated from other congeners by both external and internal morphologies. Phylogenetic analysis using partial cytochrome oxidase *c* subunit I (COI) gene shows that *Marsenina pax* new species together with *Marsenina zadei* Behrens, Ornelas, and Valdés, 2014 form a well-supported clade.

Additional Keywords: Mollusca, Velutininae, Taiping Bay, Qingdao, tunicate, ascidian, COI

INTRODUCTION

The genus *Marsenina* Gray, 1850 includes a small group of velutinid gastropods that were known from temperate waters of the Northern Hemisphere (Gulbin and Golikov, 2000). Within the family, *Marsenina* is characterized by having radula with a formula of 2+1+1+1+2, being hermaphroditic, and having a fissure or pore in the mantle exposing the shell (Gray, 1850; Bergh, 1886; Behrens et al., 2014). To date, a total of seven species ascribed to *Marsenina* have been described from North Pacific (Dall, 1871; Habe, 1958; Behrens et al., 2014), North Atlantic (Couthouy, 1838; Verrill, 1880; Perry, 1939), and Arctic regions (Gulbin and Golikov, 2000). The genus was found from the intertidal zone to the upper bathyal zone (~1222 m, represented by *M. glabra* (Couthouy, 1838)). The greatest diversity of species is found in the North Pacific, where four out of seven species are recorded, including *M. uchidai* (Habe, 1958) from the Bering Island to the northern part of the Sea of Japan, *M. rhombica* (Dall, 1871) from the Sea of Japan to Monterey Bay, and *M. stearnsii* (Dall, 1871), and *M. zadei* Behrens, Ornelas, and Valdés, 2014 from British Columbia to California. Although most velutinid species live among algae, sea grasses, hydroids, sponges, ascidians, with which their way of life is closely connected (Gulbin, 2005), members of this family are specialized predators of ascidians that closely associate with their prey (Behrens, 1984; Sargent et al., 2019). They are also known to bury their eggs capsules in the tunic of the ascidians (Dias and Delboni, 2008). This close relationship has even been described as a symbiotic relationship (Queiroz and Sales, 2016). The genus *Marsenina* is not an exception. For instance, Page (2002) collected two individuals of *M. stearnsii* from a rock encrusted with the ascidian *Tridemnum opacum* (Ritter, 1907), into which the egg capsules were embedded. Behrens et al. (2014) reported *M. zadei* from an encrusting compound ascidian, tentatively identified as *Tridemnum opacum*; collected with the specimens were the salmon-orange egg capsules, which were buried in the tunic of the ascidian hosts.

Recently, three velutinid gastropods were collected from the Taiping Bay of Qingdao, China, and sent to the Institute of Oceanology, Chinese Academy of Sciences (IOCAS) for further study. Morphological and genetic analysis revealed that they represent a hitherto undescribed species belonging to the genus *Marsenina*. In the present study, we formally describe it as *Marsenina pax* new species and compare it with its congeners.

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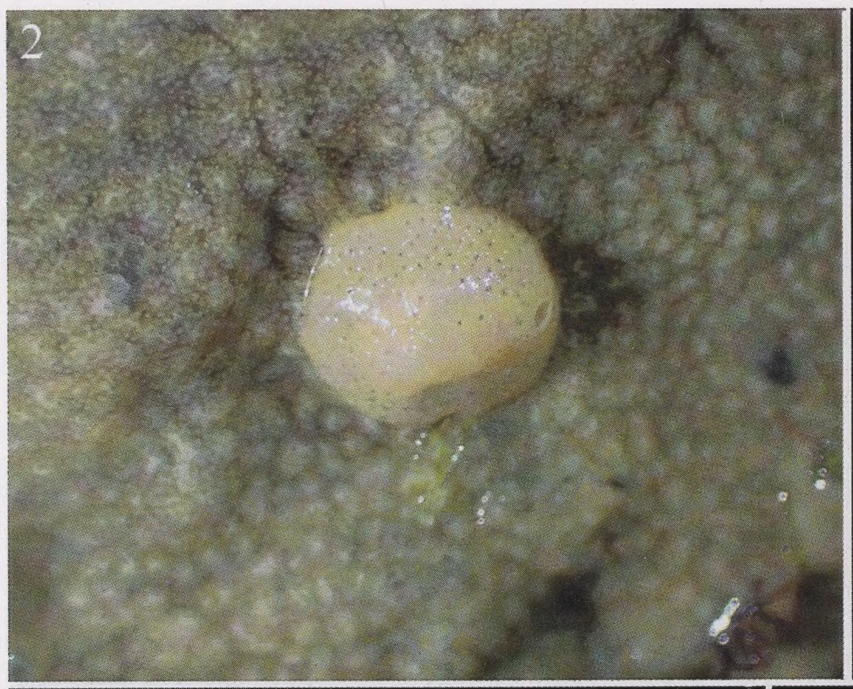
Figures 1. Map of sampling site of *Marsenina pax* new species in the Yellow Sea. Red triangle: 36°05′ N, 120°35′ E.

MATERIALS AND METHODS

Collection and Preservation: Specimens were collected alive from the lower intertidal zone of Taiping Bay in Qingdao, China (Figure 1). Specimens were photographed *in situ* and alive, and then were preserved in 75% ethanol for further study. Type specimens were deposited at the Marine Biological Museum of Chinese Academy of Sciences (MBMCAS).

Light and Scanning Electron Microscopies: Shells and soft parts were examined via light microscopy. For Scanning Electron Microscopy (SEM) studies, jaws and radula were extracted from the buccal mass by gross dissection, cleaned using 10% NaOH, rinsed in distilled water, air-dried, coated with gold, and examined with Hitachi S–3400N SEM at an accelerating voltage of 5kV.

Molecular Analyses: Genomic DNA of the three specimens was extracted with the Column Genomic DNA Isolation Kit (Beijing TIANGEN, China) according to the manufacturer's instructions. DNA was eluted in elution buffer and stored at –20°C until use. The partial COI was amplified by polymerase chain reaction (PCR) using the primers LCO1490 (forward: 5′-GGTCAACAAATCATAAAGATATTGG-3′) and HCO2198 (reverse: 5′-TTAACTTCAGGGTGACCAAAAAATCA-3′) (Folmer et al., 1994). PCR reactions were carried out in a total volume of 50 µL, including 2 µL DNA template, 1.5 mM $MgCl_2$, 0.2 mM of each dNTPs, 1 µL of both forward and reverse PCR primers, 10× buffer and 2.5 U T5 DNA polymerase (TsingKe, Beijing). Thermal cycling was performed under the following conditions: 95°C for 3 min (initial denaturation), followed by 35 cycles of 95°C for 30s (denaturation), 42°C for 30s (annealing), 72°C for 60s (extension) and a final extension at 72°C for 10 min. PCR products were verified on a GelRed-stained 1.5% agarose gel and purified with the Column PCR Product Purification Kit (Shanghai Sangon, China). Purified products were sequenced in both directions using the BigDye Terminator Cycle Sequencing Kit (v. 3.1 Applied Biosystems) and an AB PRISM 3730 (Applied Biosystems) automatic sequencer. One partial COI gene was obtained from paratype 1 and was deposited in GenBank. In addition, sequences for other velutinid species were retrieved from GenBank and used for phylogenetic analyses. We used *Triviella millardi* (Cate, 1979) to root the tree. Sequence alignments were generated using Clustal W (Higgins et al., 1994) embedded in the MEGA X (Kumar et al., 2018). For phylogenetic analyses, COI sequences from the present study and those from GenBank were used. The software MEGA X was employed to calculate the pairwise distances of COI sequences using Kimura 2-parameter model. Bayesian Inference phylogenies were inferred using MrBayes 3.2.6 (Ronquist et al., 2012)



Figures 2–5. Living animal of *Marsenina pax* new species, holotype (MBM285091) and paratype 1. (MBM286523). **2.** *In situ*, attached to its host. **3–5.** In container on the shore.

under GTR+I+G+F model (2 parallel runs, 10,000,000 generations), in which the initial 25% of sampled data were discarded as burn-in. ModelFinder (Kalyaanamoorthy et al., 2017) was used to select the best-fit model using AICc criterion. Results were visualized using FigTree v. 1.4.4 (Rambaut, 2016).

SYSTEMATICS

Superfamily Velutinoidea Gray, 1840
Family Velutinidae Gray, 1840
Subfamily Velutininae Gray, 1840

Genus *Marsenina* Gray, 1850

Type Species: *Lamellaria prodita* Lovén, 1846 (= *Oxynoe*? *glabra* Couthouy, 1838)

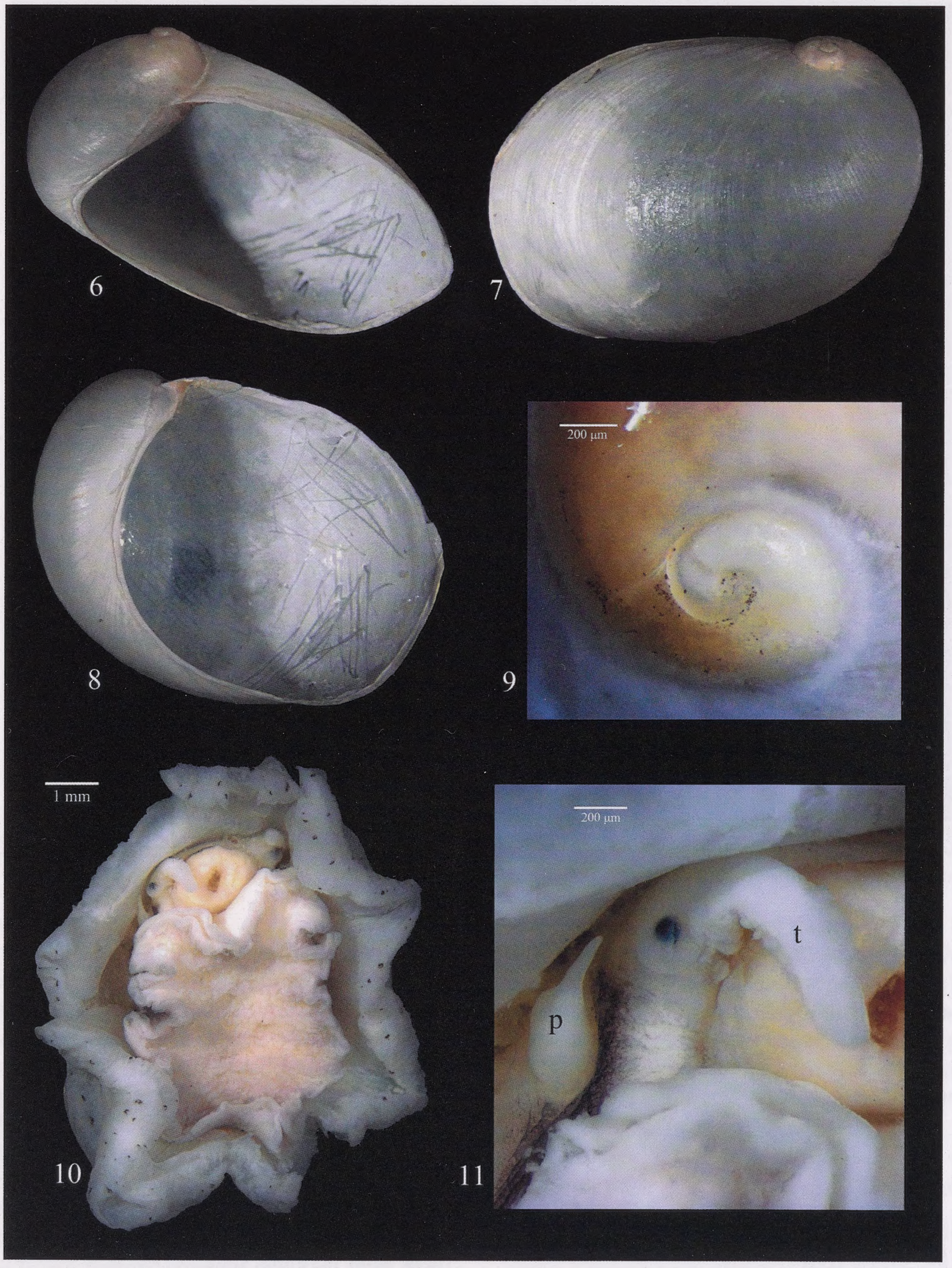
Marsenina pax new species

(Figures 2–16)

Description: External Morphology: Mantle with a dorsal pore or fissure, which can be retracted exposing shell (Figures 3–4). Mantle with an anterior and right lateral fold creating incurrent and excurrent siphons, respectively; dorsal surface generally yellowish, semitransparent, textured by several indistinct radiating yellow stripes, and numerous yellow, brown, or black spots. In one specimen, mantle marked by a longitudinal brown line lying just posterior to the anterior siphon, as well as a wide transverse brown patch on either side of fissure. Foot small, fleshy, entirely hidden under mantle; anterior edge with transverse furrow marking opening of pedal gland. Head rounded, fully covered by mantle. Cephalic tentacles long, divided into two sections; distal 1/6 relatively thin, brightly orange in color. Eyes blackish, located on short, large protuberance lateral to cephalic tentacles. Animals hermaphroditic. Penis situated posterior to right cephalic tentacle; simple, distal section tapering, with a broad proximal base (Figures 10, 11).

Shell (Figures 6–9): Shell ovate, semitransparent, with 3.25 convex whorls and deep, thin suture. Protoconch large, with about one flattened whorl, hardly elevated above spire. Last whorl large, rounded, sculptured with fine, densely spaced growth lines. Aperture broad, almost square. Outer lip thin, angulated in upper portion. Inner lip slightly thickened with weak callus. Shell white, surface covered with rather thin translucent-white periostracum.

Jaw and Radula: Jaw composed of numerous rows of scale-like elements; masticatory border with a series of uniform denticles (Figures 12–14). Radular formula of 2+1+1+1+2 (Figures 15, 16). Rachidian tooth bearing one



Figures 6–11. *Marsenina pax* new species, holotype (MBM285091). **6–8.** Different views of shell. **9.** Protoconch. **10.** Ventral view of soft parts. **11.** Right tentacle (t), and penis (p).

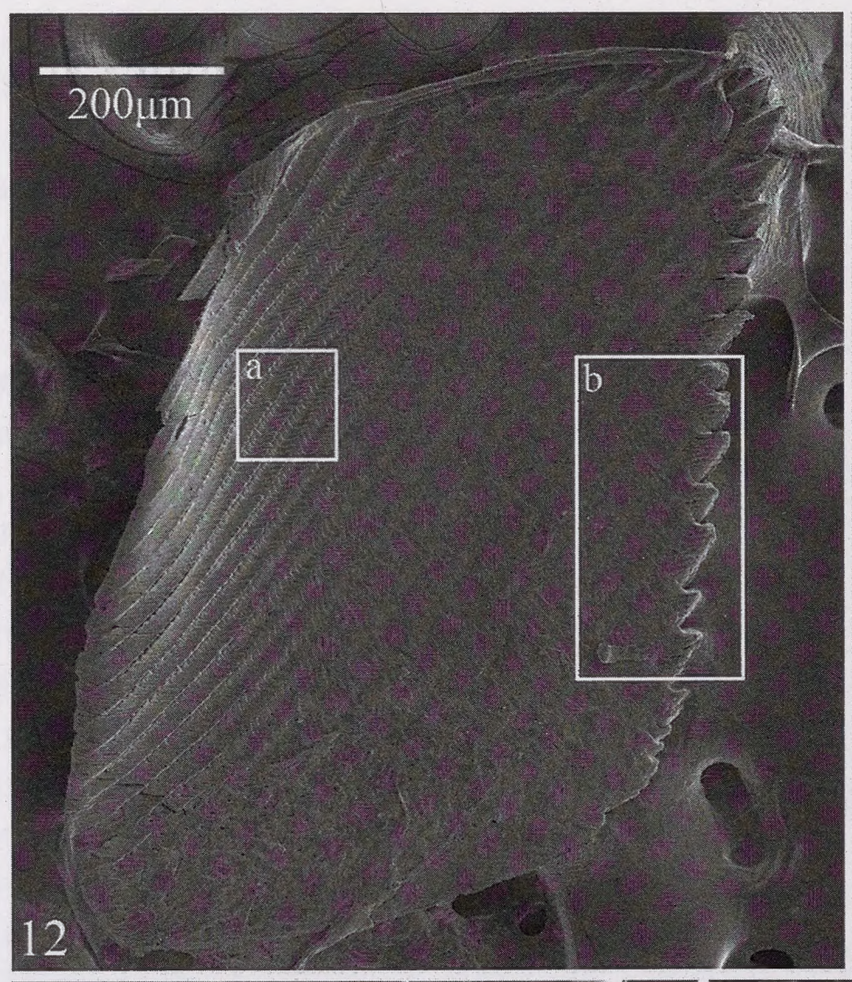
strong, triangular denticle on each side of elongate central cusp. Lateral teeth bearing a single, strong denticle on each side of wide, triangular central cusp. Marginal teeth hook-shaped, bearing one denticle situated on inner edge.

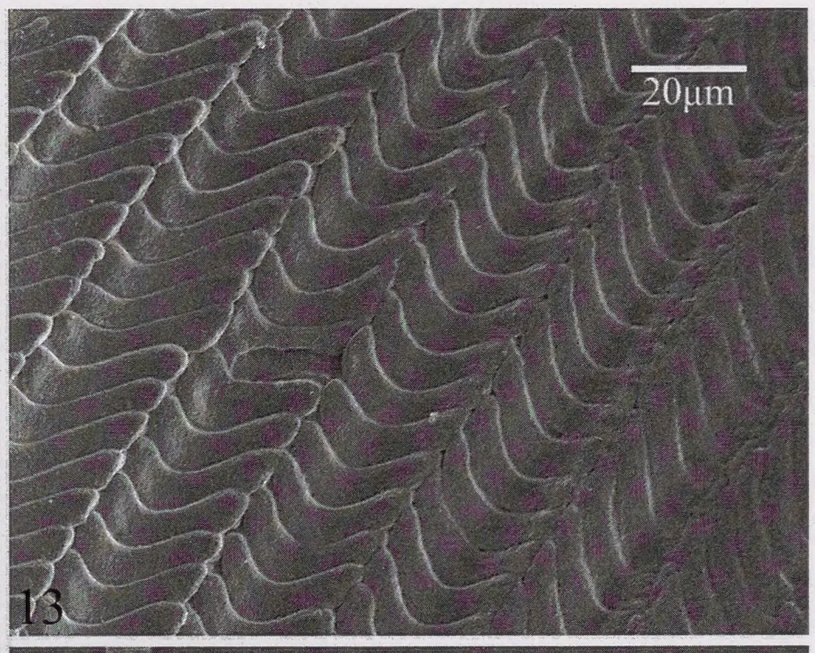
Biology: All specimens were discovered on an encrusting compound ascidian, tentatively identified as *Botrylloides* species, in the lower intertidal zone.

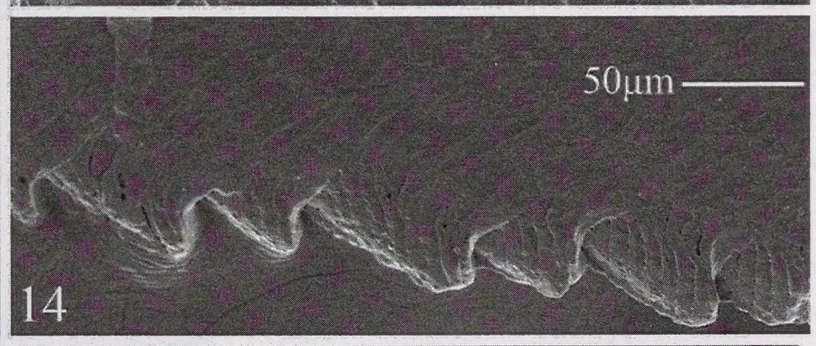
Type Material: Holotype, dissected, MBM285091, 12.0 mm preserved length; Paratypes 1 (MBM286523) and paratype 2 (MBM286511), both 10.5 mm preserved length, all collected by the third author in 20 July 2020, from type locality.

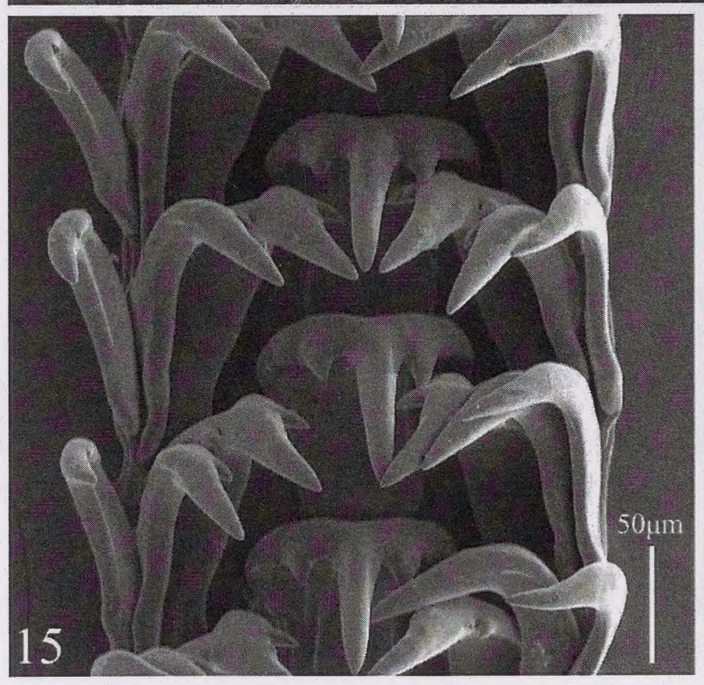
Type Locality: Intertidal zone of Taiping Bay, Qingdao (36°05′ N, 120°35′ E).

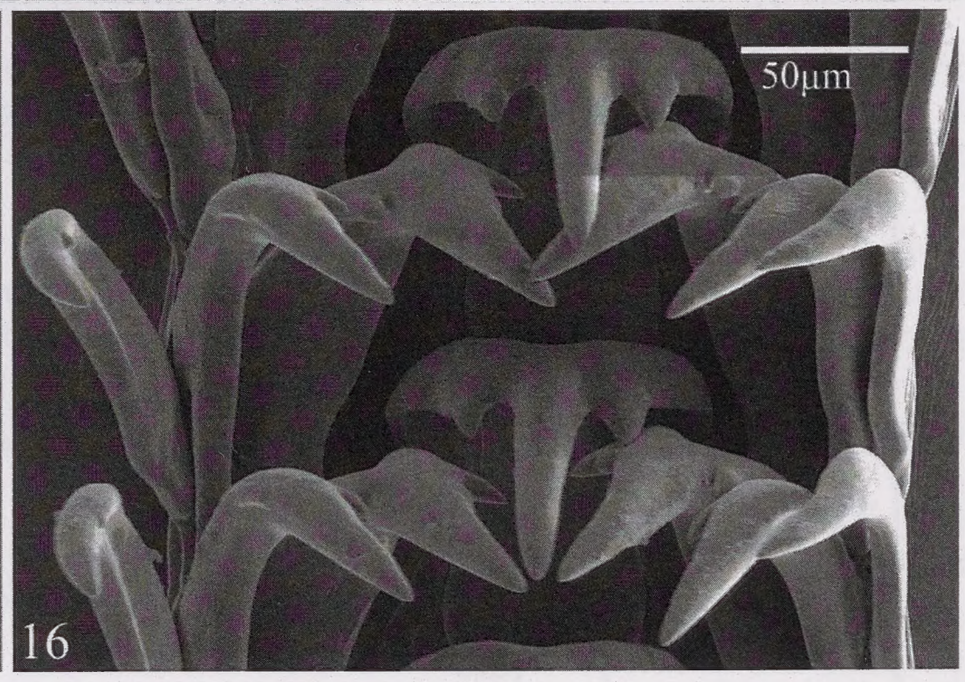
Etymology: *Pax*, Latin noun meaning peace, referring to the type locality Taiping Bay. Taiping in Chinese means peace. Used as a noun in apposition.



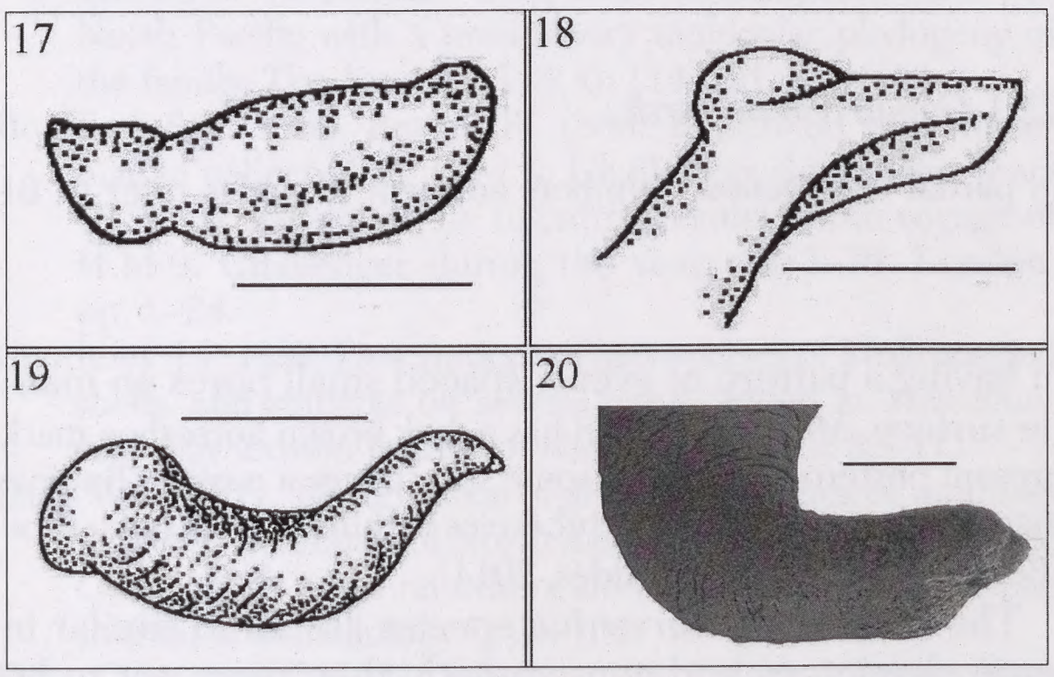








Figures 12–16. Jaw and radula of holotype (MBM285091). **12.** Right jaw. **13.** close-up of rectangle a. **14.** close-up of rectangle b. **15, 16.** Dorsal view of intact radular segment.



Figures 17–20. Available penis morphology of four other *Marsenina* species. **17.** *Marsenina glabra*, after Gulbin and Golikov (2000): 146, fig. 5d; **18.** *Marsenina uschidai*, after Gulbin and Golikov (2000): 147, fig. 6d; **19.** *Marsenina rhombica*, after Gulbin and Golikov (2000): 147, fig. 7d; **20.** *Marsenina zadei*, after Behrens et al. (2014): 117, fig. 10. Scale bar = 500 µm.

Remarks: The new species described herein is characterized by a radula having a formula of 2+1+1+1+2, being hermaphroditic, having a fissure or pore in the mantle exposing the shell. Based on these features, we allocate this species in the genus *Marsenina* Gray, 1850. This allocation is supported by molecular evidence. Due to lack of COI sequences for other *Marsenina* species, the present molecular study can only confirm the generic placement of the new species, and the fact that this species is genetically distinct from *M. zadei* Behrens, Ornelas, and Valdés, 2014. Within the genus, *M. pax* new species can be clearly distinguished from four other species from the North Pacific by both external and internal features. The penis morphology is so far known only for four species (see Figures 17–20). Like *M. pax* new species, *M. rhombica* (Dall, 1871) has a simple penis, but the shape of penis in this species is horn-shaped (see Figure 19), not distally pointed with a broad base as described for *M. pax* herein. *Marsenina uchidai* (Habe, 1958) has a beaked

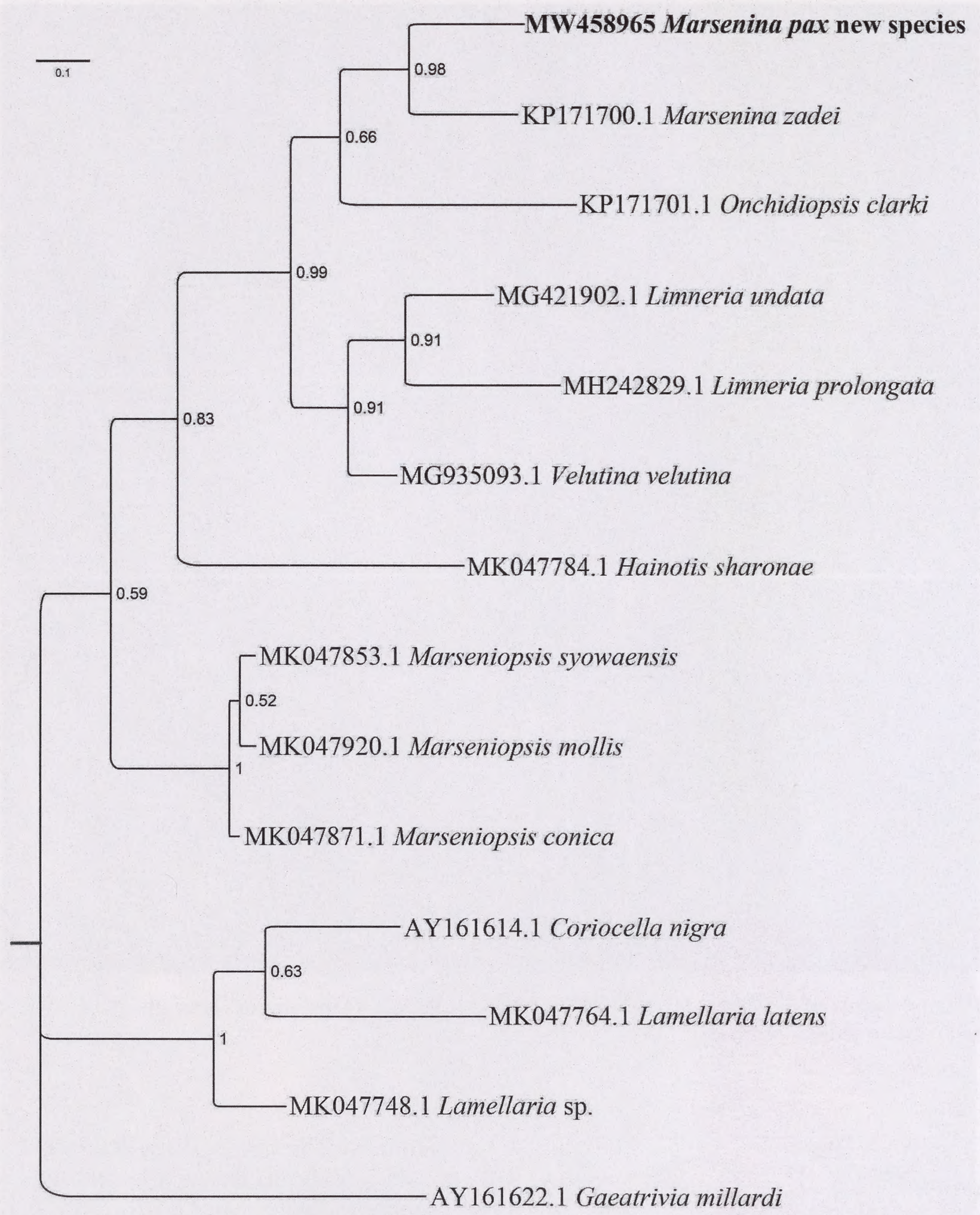


Figure 21. Phylogenetic tree inferred by Bayesian analysis (BI) from partial COI genes. Numbers adjacent to nodes refer to BI posterior probability.

penis with a bent distal end, and a crest near the bent (see Figure 18); *M. zadei* Behrens, Ornelas, and Valdés, 2014 has a penis that branch into three blunt apices distally (see Figure 20).

Okutani (2000) illustrated the living animals of *M. uchidai* (Habe, 1958). They have similar general coloration to *M. pax* new species, but differ in having numerous large rounded tubercles on the dorsal surface. Behrens (1980) reported that the mantle of *M. rhombica* varies from smooth to warty, having variable color from translucent, gray or yellow, to orange, with different degrees of spotting, specking, or blotching. However, this species lacks any radiating yellow stripes as present in *M. pax* new species. *Marsenina stearnsii* (Dall, 1871) differs in having a pattern of evenly spaced small pores on mantle surface. *Marsenina zadei* has a dark brown horseshoe mark present postero-medially in some specimens; a most distinctive mantle feature is a series of tubercles within the dark horseshoe (Behrens, Ornelas, and Valdés, 2014).

The radulae of *Marsenina* species are all so similar in basic characters, and consequently they seem not to be appropriate for clear species delimitation. The radular teeth morphologies in *M. rhombica* and *M. stearnsii* were found to be identical and differs slightly from that of *M. zadei* (see Behrens, 1980; Behrens et al., 2014). Some intraspecific variations were also recorded; the marginal teeth of *M. rhombica* were described as hamate by Behrens (1980), but reported to be simple by Gulbin and

Golikov (2000). *Marsenina uchidai* (Habe, 1958) differs slightly from these three species in having a rachidian tooth with 2 or 3 (instead of 0–1 or 1–2) denticles lateral to the central cusp. *Marsenina pax* new species have rachidian tooth with a long slender central cusp and one large denticle lateral to each side of the central cusp.

Molecular Analyses: One partial sequence for the COI region from the paratype 1 was successfully amplified and sequenced, and has been deposited in GenBank (Accession number: MW458965). The length of the partial COI sequence of the new species is 619 bp. The Bayesian phylogenetic tree (Figure 21) was reconstructed using available COI sequences from this study and GenBank. The alignment of COI had a total of 575 bp. The phylogenetic tree shows that within the family, *Marsenina pax* new species together with *M. zadei* Behrens, Ornelas, and Valdés, 2014 form a well-supported clade (PP=0.98). The uncorrected p-distance between *M. pax* and *M. zadei* was 15.1% in 575 bp of the COI gene. With the available sequences from GenBank, the pairwise distances among *M. pax* and other velutinid species range from 18.8–30%.

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The genera *Tetrarca* (Subfamily Cuculaeinae), *Arca,* and *Lamarcka*, new genus (Subfamily Arcinae), with special reference to the history of cold adaptation in North Pacific *Tetrarca boucardi* (Bivalvia: Arcidae)

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ABSTRACT

Adaptation to cold shallow water characterizes several lineages in the bivalve family Arcidae. One of these, *Arca boucardi* Jousseaume, 1894, differs from *Arca* Linnaeus, 1758 both morphologically and in molecular characters. Here we formally propose that this northwest Pacific species, along with several other fossil and extant species, belongs to the cold-water genus *Tetrarca* Nordsieck, 1969 in the Cucullaeinae. In addition, we re-examine the genus *Arca* and propose the new genus *Lamarcka* for *Arca avellana* Lamarck, 1819 and related tropical species. *Tetrarca* is inferred to have a southern-hemisphere origin. The extant *T. boucardi* is inferred to have migrated to East Asia from the northeast Pacific, where the genus *Tetrarca* became extinct in the early Pleistocene. Cold adaptation in *T. boucardi* and in *Scapharca broughtoni* Schrenck, 1867 took place in the northwest Pacific.

Additional Keywords: Neogene, cold water, temperate

INTRODUCTION

Many clades of primarily warm-water species contain lineages that have become adapted to cold water. The question where, when, and how cold adaptation was achieved is important in light of the fact that thermal tolerances of species tend to be highly conservative, and that many species today must contend with a rapidly changing climate. Most speciation events take place within rather than between climatic zones, indicating that transitions from one thermal regime to another are relatively infrequent, and that most lineages do not make them. In order to answer questions about cold adaptation, it is necessary first to identify the correct phylogenetic position of lineages that have made the transition to cold climates, and then to establish the location and timing of change and the potential for dispersal of the new lineage to other similar climatic regions elsewhere (Vermeij, 2018; Vermeij et al., 2019).

The bivalve family Arcidae is a group in which adaptation to cold conditions can be fruitfully studied. The combination of a rich fossil record and a robust phylogenetic hypothesis for the family (Combosch and Giribet, 2016; Feng et al., 2015; Kong et al., 2020) makes it possible to infer the origins of cold-water lineages. Among shallow-water marine arcids, warm-temperate lineages of Neogene members of the subfamily Anadarinae have already been documented for the North Pacific (Moore, 1983; Noda, 1966), the northwest Atlantic (Ward, 1992), and southern South America (Frassinetti and Covacevich, 1993; del Río, 1991; del Río, 1992). Temperate members of "Arcinae" are known from New Zealand (Beu, 1973), the North Pacific (see below) and southern South America (del Río, 1991; del Río, 1992). Cool-temperate shallow-water species are, however, known only in the northwest Pacific, where *Scarpharca broughtoni* became adapted to low-boreal conditions during the middle Pleistocene (Amano and Komori, 2021); *A. amicula* (Yokoyama, 1925) in the late Miocene (Amano and Koike, 1993); *Barbatia neozealanica* (Smith, 1915) in the early Pliocene to Recent of southern New Zealand; and "*Arca*" *boucardi* Jousseaume, 1894, may have done so earlier. This paper is concerned with the last species.

The genus *Arca* Linnaeus, 1758 in its traditional sense comprises tropical and subtropical species extending back to at least the middle Eocene (Reinhart, 1943). They are found in all warm seas, where they are members of epifaunal communities and are attached by a byssus. A few northern and southern cool-temperate species have also traditionally been assigned to *Arca*, including late Oligocene to Pleistocene species in New Zealand (Beu, 1973; Beu and Maxwell, 1990), Argentina (del Río, 1991; del Río, 1992; del Río and Camacho, 1998), California (Hall, 1964; Moore, 1983), and *A. boucardi* from northeast Asia. Molecular data on *A. boucardi*, however, indicate that this species in not related to *Arca* but is instead closer to the subfamily Cucullaeinae (Combosch and Giribet, 2016;

Feng et al., 2015). This species was therefore considered to be a member of the genus *Tetrarca* Nordsleck, 1969, whose type species, *Arca tetragona* Poll, 1795, extends to cold waters in the North Atlantic (Oliver and Chesney, 1994; Oliver and von Cosel, 1992). Here we reconstruct the history and taxonomy of *Tetrarca* and comment on the history and taxonomy of *Arca*, with the proposal of the new genus *Lamarcka* for one group of tropical species formerly assigned to *Arca*.

SYSTEMATICS

Family Arcidae Lamarck, 1809
Subfamily Arcinae Lamarck, 1809

Genus *Arca* Linnaeus, 1758

Type Species: *Arca noae* Linnaeus, 1758

Remarks: Species of *Arca* in its traditional sense are characterized by an equivalve, antero-posteriorly elongated shell, a wide cardinal area, beaks placed well anterior to the midline of the hinge and shell, a variably large byssal gape, and usually low radial ribs, as well as by a rather sharp postero-dorsal keel. The posterior or postero-dorsal margin is throughout sinuated. The valves are strongly inflated and the hinge line is very long and straight. The inner edge of the ventral margin is smooth around the byssal gape, and may be smooth or crenulated elsewhere. The hinge teeth are numerous and rather uniform along the length of the hinge line. The adductor muscle scars are not raised on a flange or platform.

Earlier authors identified three or four groups of species in the genus *Arca* (Huber, 2010; Lutaenko and Maestrati, 2007; Oliver and Holmes, 2006; Vermeij, 2013). One group, which contains the type species *A. noae* from the Mediterranean and West Africa, as well as other tropical species, is referred to here as *Arca* in the strict sense. It is characterized by a highly elongate shell, having a protruding posterior wing and sulcus, a pointed anterior end, a vertical posterior margin that is strongly indented, well developed radial ribs, and an inner valve margin that is usually ventrally crenulated on its posterior sector. Lutaenko and Maestrati, (2007) refer to this as their Group II. An extreme version is represented by the taxon *Arcoptera* Heilprin, 1887, containing the single species *A. wagneriana* Dall, 1898 from the early Pleistocene of Florida. In that species, the hinge line extends to a posterior point, below which the posterior margin slopes anterior to the posteroventral corner; the anterior end comes to a long, acute point. We consider *Arcoptera* to be an extreme member of *Arca*, which has assumed a semi-infaunal mode of life instead of the more typical epibyssate habit. We also include in *Arca* in the strict sense the sole member of Lutaenko and Maestrati's (2007) Group III, *Arca koumaci* Lutaenko and Maestrati, 2007. This diminutive species from the Indo-West Pacific, distinguished by a rounded ventral margin and a sharp posterior keel bearing tiny spines, resembles miniature *A. navicularis* Bruguière, 1798, an undoubted member of *Arca* s. s.

In addition to the species mentioned above, we include the following extant species in *Arca*: *A. bouvieri* Fischer, 1874, from West Africa; *A. pacifica* Sowerby, 1833 from the eastern Pacific; *A. zebra* Swainson, 1833 from the western Atlantic; and *A. symphenacis* Oliver and Chesney, 1994, from the Indo-West Pacific. Additional fossil species include *A. aquila* Heilprin, 1887, from the early Pleistocene of Florida; *A. budoensis* Amano and Kurita, 2020 from the late early Miocene of Japan; *A. noae biangulina* d'Orbigny, 1852, from the early Miocene of France; and *A. paratina* Dall, 1898 and its ancestral subspecies *A. p. tampae* Mansfield, 1937, from the early Miocene of Florida.

A second group (Group I of Lutaenko and Maestrati, 2007), typified by the Indo-West Pacific *Arca avellana* Lamarck, 1819, but also containing other tropical species, is distinct morphologically and in molecular phylogenetic analyses (Combosch and Giribet, 2016; Feng et al., 2015; Vermeij, 2013). Compared with *Arca* in the strict sense, this group is characterized by a less elongate shell in which the posterodorsal margin is obliquely rather than vertically truncated, the radial ribbing is much finer, the anterior end is rounded rather than pointed, and the inner margin of the ventral shell edge is usually smooth throughout. Lutaenko and Maestrati (2007) also included *Arca tetragona* Poli, 1795 and *A. boucardi* in this group, but we exclude them here (see below). Following the recommendation of Combosch and Giribet (2016), and given the differences with *Arca* previously noted by Oliver and Holmes (2006) and Vermeij (2013), we propose a new genus for this second group that was previously attributed to *Arca*.

Genus *Lamarcka* new genus

Type Species: *Arca avellana* Lamarck, 1819 (Recent, Indo-West Pacific).

Description: Shell anteroposteriorly somewhat elongate, anteriorly rounded, posteriorly obliquely truncate, with a generally well-marked keel from the umbones to the posteroventral corner, separating the posterior sector from the rest of the shell; sculpture consisting of fine radial ribs and imbricating growth lines, the latter particularly distinct on the posterior keel; ventral margin with a byssal gape, usually smooth throughout on its inner edge.

Etymology: Named for J.B.P.A. de Lamarck, author of the type species.

Other Included Species: RECENT SPECIES – *L. avellana turbatrix* (Oliver and von Cosel, 1992), West Africa; and the Indo-West Pacific *L. ventricosa* (Lamarck 1819); *L. angulata* (King and Broderip, 1831), *L. imbricata* (Bruguiere, 1789), western Atlantic; *L. mutabilis* (Sowerby, 1833), eastern Pacific; and *L. truncata* (Sowerby, 1833), eastern Pacific.

Figures 1–2. Two specimens of *Tetrarca boucardi*. **1.** Fossil specimen from the upper Pleistocene Anden Formation in Akita Prefecture, northern Honshu of Japan (outer and inner views). **2.** Recent specimen from Tanihama, Joetsu in Niigata Prefecture, central Honshu of Japan (outer and inner views).

FOSSIL SPECIES – *L. bowdeniana* (Dall, 1898), Pliocene, Jamaica; *L. emiliae* (Dollfus, 1909), early Miocene, France (see Lozouet et al., 2003); *L. subcontracta* (Heilprin, 1882), early Oligocene, Mississippi (see Dockery III, 1982). *L. sakamizuensis* (Hatai and Nisiyama, 1952), Oligocene, Kyushu; ? *L. uedai* (Matsubara, 2002), Paleogene, Maejima, Southwestern Honshu; *L. williamsi* (Olsson, 1967), Pliocene, Florida.

Subfamily Cucullaeinae Lamarck, 1809

Genus *Tetrarca* Nordsieck, 1969

Type Species: *Arca tetragona* Poll, 1795 (Recent, Mediterranean)

Remarks: As noted by Combosch and Giribet, (2016), *Tetrarca* differs from *Arca*, *Lamarcka* and most other Arcidae by having a posterior flange on which the posterior adductor scar is situated. This feature characterizes members of the Cucullaeinae, a group to which *Tetrarca* (as represented by *T. boucardi* (Jousseaume, 1894) (Figures 1, 2) in molecular analyses) is closely related (Combosch and Giribet, 2016; Feng et al., 2015). In addition, the ventral margin of the valves is internally crenulated (see also Vermeij, 2013) and the strong ridge from the beak to posteroventral corner.

Oliver and Chesney (1994) assigned the following extant species to *Tetrarca*: *A. tetragona* from the northeast Atlantic, ranging from West Africa north to 69.5° N (Høsæter, 1986); *T. acuminata* Krauss, 1848 from southern Africa; *T. a. dayi* Oliver and Chesney, 1994 from the upwelling zone in the Gulf of Oman; and *T. boucardi*. In addition, Oliver in Valentich-Scott et al. (2020) assigned *Arca fernandezensis* Hertlein and Strong, 1943, from the Juan Fernandez Islands, Chile, to *Tetrarca*. The genus *Tetrarca* therefore occurs in cool waters in both the northern and southern hemispheres.

DISCUSSION

Until now, the fossil record of *Tetrarca* had not been systematically investigated. Marquet (2002) summarized fossil occurrences of *T. tetragona*, and noted that this species is known as early as the Tortonian (late Miocene) of Portugal and also occurs in the Pliocene of the North Sea Basin. In the northwest Pacific, *T. boucardi* is recorded (as *Arca praeboucardi* Sinel'nikova in Gladenkov and Sinel'nikova, 1990) from the lower middle Miocene Kakert and Ilyin horizons of Kamchatka (Gladenkov et al., 1984; Gladenkov and Sinel'nikova, 1990), as well as from the lower Miocene and many younger formations in Japan (Noda, 1966). No earlier species have been recorded from temperate East Asia.

In the northeast Pacific, two definite and one possible species can be confidently attributed to *Tetrarca* from the Cenozoic of western North America. These are *Arca leptogrammica* Hall, 1964 from the Santa Margarita Formation (early middle Miocene; Prothero, 2001) of San Luis Obispo County, California, and *A. sisquocensis* Reinhart, 1937 from the Pliocene and Pleistocene of southern California. Woodring in Woodring and Bramlette (1950) and Hall (1964) had already drawn attention to the similarities of these two species with *T. boucardi* (see also Moore, 1983). Both taxa have the essential features of *Tetrarca*. A possible third member of *Tetraca* from western North America is the small-bodied *Arca washingtoniana* Dickerson, 1917 from the Gries Ranch Formation (latest Eocene;

Prothero, 2001) of Washington State (see Weaver, 1942, and Durham, 1944 for good descriptions). There is no living species assignable to *Tetrarca* in the northeast Pacific.

We hypothesize that the northwest Pacific *T. boucardi* arose from a lineage that originated in the warm-temperate northeast Pacific. The ancestor of *T. boucardi* would have migrated westward during or just before the early Miocene, when ocean temperatures across the North Pacific were relatively warm. Cold adaptation in *T. boucardi* likely took place soon thereafter given that the early records of this species are what were even then cold-temperate conditions in Kamchatka (Kafanov and Volvenko, 1997). In the northeast Pacific, *Tetrarca* remained in warm-temperate conditions until its regional extinction in the early Pleistocene.

This biogeographical pattern of early Miocene westward migration of lineages from the northeast Pacific to East Asia is consistent with the history of numerous other molluscan groups (for summaries see Amano and Kurita, 2020; Vermeij et al., 2019). Many of these groups, including *Tetrarca*, adapted to cold-water conditions in the northwest Pacific rather than in western North America.

As noted above, *Tetrarca* occurs in the temperate zones of both hemispheres. It is therefore instructive to ask how this distribution was achieved, and in particular how *Tetrarca* came to occupy the North Pacific. A possible southern-hemisphere origin of *Tetrarca* is indicated by several species in the temperate late Paleogene and Neogene faunas of New Zealand and Argentina. In Argentina, two species that were tentatively assigned to the subgenus *Eonavicula* Arkell, 1929 have the hinge and muscle-scar characteristics of *Tetrarca*. These are *Arca* (*Eonavicula?*) *patagonica* von Ihering, 1897 from the Monte Leon Formation (late Oligocene) and *A.* (*E.?*) *puntaensis* del Rio and Camacho, 1998 from the San Julian Formation (late Eocene) (see del Río and Camacho, 1998). These taxa resemble species assigned to *Arca* from New Zealand, collectively ranging from the late Oligocene to the early Pleistocene (see Beu, 1973; Beu and Maxwell, 1990). Pending examination of these southern-hemisphere species, we suggest that they belong to *Tetrarca* rather than to the primarily Mesozoic taxon *Eonvavicula*, and therefoore that the genus *Tetrarca* originated from some cucullaeine ancestor in the southern hemisphere during the Paleogene. In this connection it is interesting to note that the Cucullaeinae, a primarily Mesozoic subfamily (Nicol, 1954), persisted to the middle Miocene in Chile (Frassinetti and Covacevich, 1993) and the late Oligocene of Argentina (del Río and Camacho, 1998). The genus *Cucullaea* Lamarck, 1801 is today represented by one or two Indo-West Pacific species, but it has a broader distribution, including the southern (but not northern) hemisphere during the Paleogene. The shells of most cucullaeines are much less antero-posteriorly elongate than in *Tetrarca*, but they share with *Tetrarca* the well-developed posterior adductor flange and the ventrally crenulated margin. If this scenario is correct, *Tetrarca* would represent a strong case of convergence with *Arca* and *Lamarcka*, and would imply a transition from infaunal to epifaunal habits. Like a number of other lineages with a temperate southern-hemisphere origin, *Tetrarca*'s spread to the North Pacific would have occurred during the latest Eocene, when the eastern Pacific tropics were likely cooler than they are today (Vermeij et al., 2019).

The origin of the North Atlantic *T. tetragona* remains obscure, but may indicate a second northward dispersal in the genus. If *Tetrarca* originated in the southern hemisphere, *T. fernandezensis* and *T. acuminata* would represent relicts of a once more widely distribution that included Argentina and New Zealand. *T. tetragona* would then be the result of dispersal from southern Africa northward. Vermeij (1993) proposed a similar northward dispersal for the extinct muricid gastropod genus *Spinucella* Vermeij, 1993, part of a larger clade of Ocenebrinae with presumed southern-hemisphere origins that also includes a number of North Pacific genera.

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Asymmetrical sculpture in Arcidae (Bivalvia), with comments on the genera *Caloosarca* and *Cunearca* (Bivalvia: Arcidae)

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ABSTRACT

The Arcidae is a well-known and diverse family of bivalves, but variations in shell sculpture among its members have been little studied. Two types of asymmetrical sculpture are here documented in Arcidae: imbricate periostracal and concentric shell sculpture, in which the abumbonal slopes are steeper than the adumbonal slopes; and ratchet sculpture, in which the adumbonal slopes are steeper. Imbrication is widespread on parts of arcid shells at and above the sediment or rock surface. The genus *Caloosarca* Olsson, 1961, which is here revised to include only a group of Pliocene and Pleistocene species from the southeastern United States, is unusual among infaunal bivalves in having strongly imbricate concentric sculpture over the whole shell. Anterior ratchet sculpture Is here documented for the first time in the genus *Cunearca* Dall, 1898, which is here restricted to include species from tropical and subtropical American waters.

Additional Keywords: ratchet sculpture, imbricate sculpture

INTRODUCTION

The Arcidae is a taxonomically and ecologically diverse family of Jurassic to Recent bivalves found in tropical to cold-temperate seas from the intertidal zone to bathyal depths, as well as in South Asian freshwater (Mienis and Ritter, 2016; Oliver and Holmes, 2006). In life habits, arcids vary from being byssally attached on hard surfaces or partially buried in sediment to endolithic (the genus *Litharca* Gray, 1842, boring into rocks in the tropical eastern Pacific) and fully infaunal (burrowing) in sand or mud. Shells may be equivalve, with the left and right valves similar in size and sculpture, or inequivalve, with the left valve typically larger than and overlapping the right valve and often differing in sculpture from the latter. The commissure typically lies in one plane, but at least three lineages (*Trisidos* Roding, 1798; *Ambrogia* La Perna, 2007; and *"Anadara" campyla* Dall, 1898) have twisted valves whose commissure traces a three-dimensional curve (Dall, 1898; McGhee, 1978; Tevesz and Carter, 1979; Savazzi, 1981; Morton, 1983; La Perna, 2006). The valve edge may be internally smooth, crenulated or plicated, and projections of the ventral and posterior margins, when present, are always formed by extensions of the radial ribs rather than their interspaces (Vermeij, 2013). Functional studies have pointed to adaptive limitations arising from a weak ligament (Thomas, 1978; Savazzi, 1982), which prevents rapid burrowing. No burrowing arcids are rostrate, indicating that there are no deep-burrowing species and pointing to the absence of siphons (see also Stanley, 1968).

The arcid shell is divisible into three sectors that differ in surface sculpture. The posterior sector is set off from the central sector by a variably developed angulation or keel that extends from the umbo to the posteroventral corner. The central and anterior sectors are not as clearly demarcated from each other, but differ in the prominence of both radial and concentric sculpture. This tripartite structure appears to characterize all members of the Arcidae in the broad sense, and may represent three genetic-developmental domains of shell formation.

Arcid shell sculpture almost always features radial and concentric elements. Stanley (1970) observed that infaunal arcids are more prominently radially ribbed than epifaunal or semi-infaunal species, and that infaunal burrowers are slow and lack shell features that enhance burrowing. In particular, there are no reported cases in Arcidae of ratchet sculpture, in which the adumbonal slopes of concentric elements are steeper than the abumbonal slopes. The well-developed radial sculpture of infaunal arcids instead stabilizes the animal in the sediment (Stanley, 1970). Divaricate, oblique and spiny elements—common in many other bivalve groups—are also unknown in arcids (Thomas, 1978, 1978; Oliver and Holmes, 2006). A variably thick, hairy periostracum potentially modifies the underlying shell sculpture, especially in the posterior sector of the shell. Its evolution has been linked to the absence of spines (Harper, 1997).

Close examination of arcids in my research collection reveals two types of concentric sculpture that have either never been reported in the family (ratchet sculpture) or

have been mentioned only in passing (imbricate sculpture). Imbrication in concentric elements is characterized by having the abumbonal slopes steeper than the adumbonal slopes. The asymmetry of imbricate sculpture is therefore opposite to that of ratchet sculpture. Imbricate concentric sculpture is particularly obvious, but was never previously mentioned, in Pliocene and Pleistocene species of the genus *Callosarca* Olsson, 1961.

The purpose of this paper is to describe imbrication in *Callosarca*, to conduct a preliminary survey of imbricate sculpture in Arcidae, and to highlight the occurrence of ratchet sculpture in a few burrowing arcids of the genus *Cunearca* Dall, 1898. In addition, I amend the diagnosis of *Callosarca* and comment on the scope of the genus *Cunearca*.

MATERIALS AND METHODS

For the analysis of imbricate sculpture in *Callosarca*, I examined and measured the density of imbricate concentric ridges in one specimen of *C. catasarca* (Dall, 1898) and eleven valves of *C. crassicosta* (Heilprin, 1887) from the Caloosahatchee Formation of Florida. In addition, I examined about 200 lots representing 62 species of extant arcids and fossil material of 15 species from the Chipola Formation (early Miocene) of Florida, Choptank and St. Mary's Formation (middle and late Miocene respectively) of Maryland, the Gatun Formation (middle to late Miocene) of Panama, and the Plio-Pleistocene sequence in Florida encompassing the Pinecrest, Caloosahatchee, and Bermont formations.

RESULTS

Imbrication in *Caloosarca*

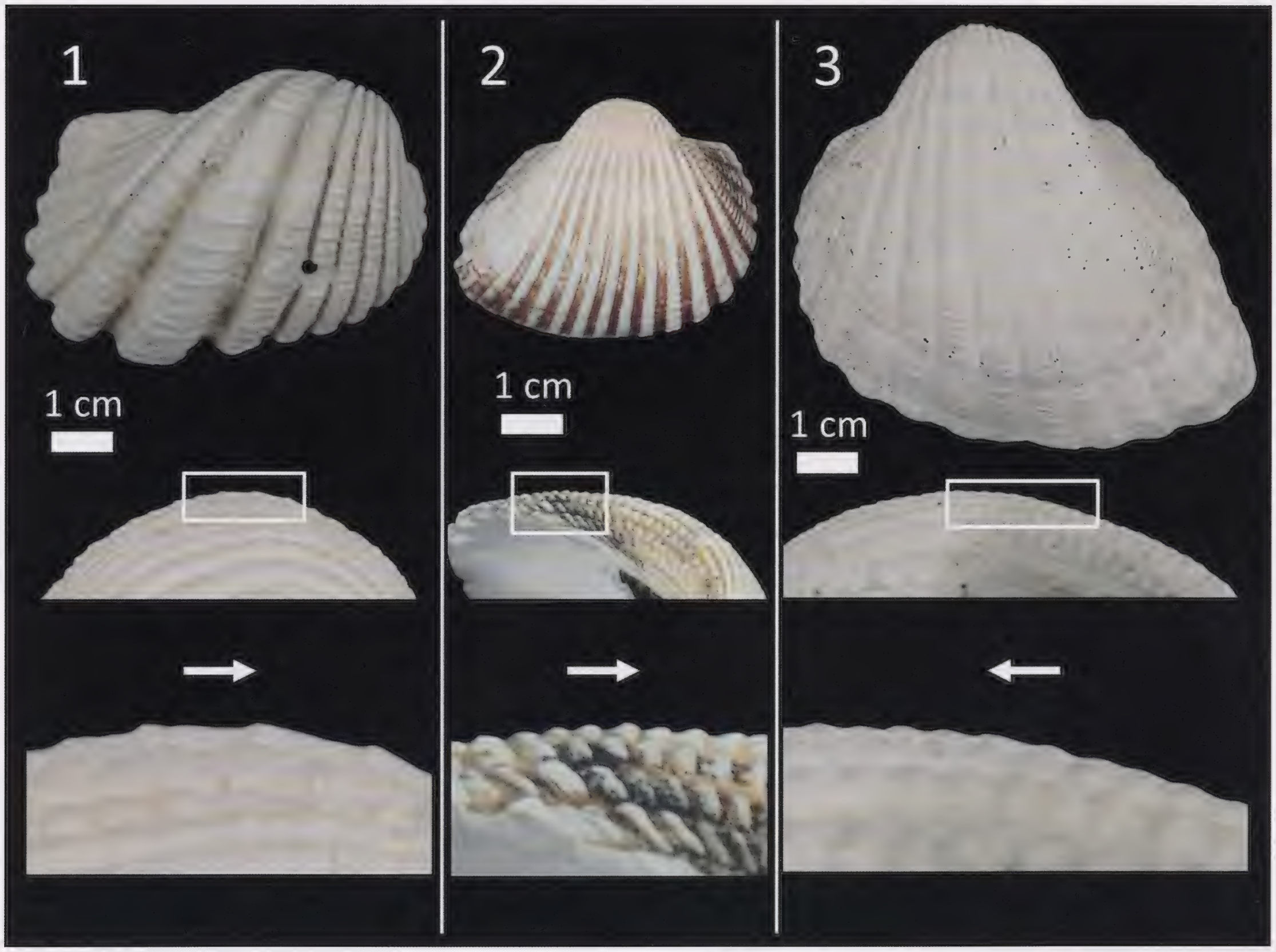
The genus *Caloosarca* is highly unusual among sediment-burrowing anadarine arcids in having conspicuously imbricated concentric ridges (Figure 1). These ridges span the entire valve surface, from the anterior and central sectors to the posterior sector, and occur on both the radial ribs and interspaces. In eleven valves representing eleven individuals of *C. crassicosta*, ranging in shell length from 27.8 to 64.3 mm, the average density (with standard deviation) of the imbricated concentric ridges per mm of radial length is 0.70 ± 0.085 (range 0.59 to 0.98), as measured along one of the broad ribs on the central sector of the shell from the ventral shell margin to a distance of either 34.0 mm or 17.5 mm from the margin depending on shell size. The density of concentric ridges in the single valve of *C. catasarca*, with a length of 71.7 mm, is 0.79 per mm.

Imbrication in other Arcidae

Imbricate surface features are surprisingly widespread in Arcidae. Bottjer and Carter (1980) observed shingled periostracal projections in arcoideans, especially in infaunal species, and suggested that these projections increased the force of dislodgement from the sediment, and perhaps prevented bioerosion and drilling predation. García and Oliver (2008) described periostracal bristles and hairs as appressed to the valve surface with their ends pointing distally, giving the shell an imbricate texture. They specifically mentioned this condition in the Indo-West Pacific species *Barbatia decussata* (Sowerby, 1833), *B. foliata* (Forsskal, 1775), *B. grayana* (Dunker, 1858), and *B. (Savignyarca) virescens* (Reeve, 1844) (see also Lamprell and Healy, 1998). The late Eocene to Recent genus *Asperarca* Sacco, 1898 from deep water has distinctly lamellose concentric shell sculpture whose abumbonal edges give the shell an imbricate appearance (Francisco et al., 2012; Berezovsky, 2014). Similar imbrication has been described in species of *Acar* Gray, 1857 (Lamprell and Healy, 1998; Berezovsky, 2014). Dall (1898) mentioned imbricate concentric sculpture in fossil species including *Arca bowdeniana* Dall, 1898, *A. paratina* Dall, 1898, *Barbatia (Calloarca) ireegularis* Dall, 1898, and *B. (C.) arcula* Heilprin, 1887; and Marquet (2002) describes imbricating scales in *Tetrarca tetragona* (Poll, 1795). Beyond these descriptions, there has been no systematic account of imbrication in Arcidae. Concentric shell sculpture is typically characterized as nodulose, resulting in a beaded or decussate texture where it intersects with the radial ribs.

The survey of Arcidae in my collection reveals that imbrication occurs in all byssally attached arcids examined. Periostracal elements are most conspicuously imbricated on the posterior sector of the valves, although it is subtle in thin-shelled species of *Calloarca* Gray, 1857. Imbricate concentric shell sculpture occurs on the posterior and central sectors of uneroded valves and is particularly well marked in species of *Acar*, Arca Linnaeus, 1758 in the broad sense, and *Barbatia* Gray, 1842, in the broad sense. No trace of imbricate sculpture remains on the central sector of many individuals, especially large ones, which are often tightly wedged in cracks and crevices. Posterior imbrication, however, remains conspicuous in most shells, especially on the angulation or keel separating the posterior from the central sector.

In most burrowing species of Noetiinae and Anadarinae, imbrication is confined to the periostracum on the posterior sector of the shell (see also Savazzi, 1982). I have not detected imbricate periostracum in species of *Cunearca*, a genus in which the periostracum is very thin or entirely lacking. Except in *Caloosarca*, imbricate shell sculpture is absent in Anadarinae, and develops as closely spaced growth lines on the posterior sector in the noetiine genus *Eontia* MacNeil, 1937. Beads, nodules and nodes are common ornaments on radial ribs in Anadarinae and Noetiinae, but these are generally not asymmetrical even in strongly sculptured taxa such as *Tegillarca* Iredale, 1939. Some anadarines, such as the West African *Senilia senilis* Linnaeus, 1758) lack concentric ornament altogether.



Figures 1–3. Imbrication and ratchet shell structures in various Arcidae. Arrows point towards the umbo in the closeup views. **1.** Imbrication sculpture in *Caloosarca crassicosta*. **2.** Ratchet sculpture in *Cunearca brasiliana*. **3.** Ratchet sculpture in *Cunearca scalerina*.

Ratchet Sculpture in Arcidae

Until now, ratchet (or burrowing-enhancing) shell sculpture has not been reported in the Arcidae. Here I can confirm its occurrence on the anterior valve sector of inequivalve species that I would assign to *Cunearca* (Figures 2, 3). Nodules on anterior ribs are directed slightly adumbonally in at least the following species: *C. brasiliana* (Lamarck, 1819) from the western Atlantic; *C. aequatorialis* (d'Orbigny, 1846), *C. bifrons* (Carpenter, 1857), and *C. nux* (Sowerby, 1833) from the eastern Pacific; *C. scalarina* (Heilprin, 1887) from the Caloosahatchee Formation (early Pleistocene) of Florida; and *C. initiator* (Dall, 1898); and *C. staminata* (Dall, 1898) from the Chipola Formation (early Miocene) of Florida. The shell edge in the anterior sector of the valves in these species is polished, indicating that the mantle margin crosses the shell edge in this sector when shell precipitation occurs. In parts of the shell without ratchet sculpture, and in other anadarines in which ratchet sculpture is absent, the shell edge is sharp and not polished.

DISCUSSION

The widespread occurrence of imbrication in arcids, especially on parts of the shell at or above the sediment or rock surface, is noteworthy and not previously appreciated. Although a broad survey of imbrication is beyond the scope of this paper, imbrication appears to be widespread in the major bivalve clade Pteriomorphia, to which the Arcidae belong, as well as in epifaunal carditids among the Palaeoheterodonta.

The significance of imbrication in Arcidae remains unclear. Imbrication may simply reflect the method by which new shell material is added at the valve margins during growth. In this connection it is notable that the valve margins of arcids and most other pteriomorphians are sharp, implying that the mantle margin does not cross the valve edge when fully extended. Nevertheless, the sharp valve edges of anadarines are not associated with imbrication, showing that imbricate sculpture is not an automatic consequence of this mode of shell accretion.

The development of conspicuous, regularly spaced imbricated concentric shell sculpture in *Caloosarca* is highly unusual not only in Arcidae, but among infaunal bivalves generally. In fact, the abumbonally steep slopes of imbricate concentric ridges would seem to interfere with burrowing because it adds friction as the animal moves downward into the sediment. The very high radial ribs and deep broad interspaces of *Caloosarca* indicate very sluggish burrowing in members of this genus, and a stabilizing and anchoring function for the ribs in coarse sediment. Whether and how imbricate concentric ridges contribute to this stability is unclear. Given the regular spacing of the ridges, some as yet unknown adaptive function of imbrication in *Caloosarca* cannot be ruled out.

Ratchet sculpture is uncommon, and previously overlooked, in burrowing anadarine arcids. Where it occurs in the genus *Cunearca*, it is associated with a highly inflated, anteroposteriorly short, inequivalve shell that superficially resembles the shells of ratcheted, equivalved members of the heterodont family Cardiidae. In contrast to its limited occurrence in the Arcidae, ratchet concentric sculpture is very widespread in warm-water cardiids, as well as in members of the Nuculanidae, Sareptidae, Lucinidae, Veneridae, and Tellinidae (Stanley, 1970, 1981, 1969; Checa and Jiménez-Jiménez, 2003). In these families, ratchet sculpture is not limited to highly inflated shells, but can develop also in relatively flat or disc-shaped shells. Ratcheted members of these families also burrow faster and often deeper than either unratcheted species or anadarines. Unfortunately, not data on burrowing are available for ratcheted Anadarinae.

Present evidence indicates that ratchet sculpture in *Cunearca* was already present by the early Miocene. The oldest species attributed to *Cunearca* is *C. silverdalensis* (Kellum, 1926) from the late Oligocene Of North Carolina (see Ward, 1992). I have not examined this species and therefore do not know whether ratchet sculpture was already present in this species. It is surprising that ratchet sculpture has remained restricted to tropical and subtropical American arcids, and that it apparently did not evolve in or spread to the tropical Indo-West Pacific, where morphological innovations in molluscan shells are frequent (Vermeij, 2012).

SYSTEMATICS

Family Arcidae Lamarck, 1809

Subfamily Anadarinae Reinhart, 1935

Genus *Caloosarca* Olsson, 1961

Type Species: *Anadara rustica* Tuomey and Holmes, 1857, by original designation.

Revised Description: Shell thick, Inflated, equivalve, with 16 to 25 radial ribs, those on central sector extremely broad and high and scalloping valve-margin; umbones one-third to one-fourth of shell length from anterior end; posterior end of shell truncate; posterodorsal valve margin often extended posteriorly as a wing, especially in young shells; concentric sculpture prominently imbricated throughout.

Remarks: When introducing *Caloosarca* as a subgenus of *Anadara* Gray, 1847, Olsson (1961) included two distinct groups of species. The core of the taxon, which I regard as a full genus, comprises six described species from the Pliocene and Pleistocene of the southeastern United States, well described by Vokes (1969). These are the Pliocene *C. hoerleae* (Yokes, 1969) from Florida and *C. rustica* (Tuomey and Holmes, 1857) from South Carolina; and the Pleistocene *C. crassicosta* (Heilprln, 1887), *C. catasarca* (Dall, 1898), and *C. aequalitas* (Tucker and Wilson, 1932) from Florida. The revised diagnosis offered above adequately circumscribes these highly distinctive fossil species. As interpreted here, the genus became extinct during or at the end of the interval represented by the middle Pleistocene Bermont Formation (see also (Petuch, 2004).

In addition to these typical species of *Caloosarca*, Olsson (1961) and Vokes (1969) assigned the extant species *Anadara notabilis* Röding, 1798, from the Gulf of Mexico and Caribbean to Brazil, to *Caloosarca*. My examination of this species reveals that the valves lack imbricate concentric sculpture and do not have the enlarged ribs on the central sector of the valves. The concentric sculpture bears small erect nodes, unlike the situation in typical *Caloosarca*. *Anadara notabilis* resembles *Caloosarca* superficially by having the dorsal margin somewhat extended as a wing and by having an emarginate posterior margin. I agree with Huber (2010) in assigning this species to *Anadara* in the broad sense. I note, however, that the type species of *Anadara*, *A. antiquata* Linnaeus, 1758 from the Indo-West Pacific, has a slightly inequivalve shell (Vermeij, 2013), whereas *A. notabilis*, like species of *Caloosarca*, is equivalve. Perhaps the taxon *Diluvarca* Woodring, 1925, which Kilburn (1983) rejects as invalid, would be a better fit. Olsson (1964) added another species in the *A. notabilis* group to *Caloosarca*, *A. (C.) mompicha* Olsson, 1964 from the Santiago Formation (late Miocene) of Ecuador. Based on a single valve, he compared his species to *A. notabilis*. These two species likely represent a tropical American clade distinct from *Caloosarca*.

Somewhat oddly, Olsson (1961) also included in *Caloosarca* the tropical eastern Pacific species *Anadara biangulata* (Sowerby, 1833). Unlike true *Caloosarca*, and *A. notabilis*, *A. biangulata* is distinctly inequivalve, and for this reason was assigned to *Scapharca* Gray, 1847 by Keen (1971). This species does not have imbricate sculpture, and its central ribs are not markedly enlarged. Coan and Valentich-Scott (2012), who rejected all generic or subgeneric divisions within *Anadara*, assigned this species to *Anadara*. It appears to be close to the western Atlantic *A. baughmani* Hertlein, 1951 (Coan and Valentich-Scott, 2012).

The name *Caloosarca* has occasionally been mentioned by subsequent authors. Kilburn (1983) synonymized *Caloosarca* in Olsson's (1961) original sense with the tropical Indo-West Pacific genus *Mabellarca* Iredale, 1939

but did not explain his reasons. Oliver and von Cosel (1992) accepted *Caloosarca* as valid, citing *A. notabilis* as a member, but did not discuss the typical species of the genus. These references to *Caloosarca* therefore refer to species that I exclude from that genus.

Genus *Cunearca* Dall, 1898

Type Species: *Arca incongrua* Say, 1822 (=*C. brasillana* (Lamarck, 1819), by original designation.

Remarks: The type species of *Cunearca*, the western Atlantic *C. brasiliana*, is distinguished not only by the ratchet sculpture on its anterior ribs, but also by much broader ribs on the central sector of the shell. In these respects, it closely resembles the much larger *C. scalarlna* (Heilprin, 1887) from the Caloosahatchee Formation of Florida as well as *C. eumeces* (Woodring, 1973) from the lower Gatun Formation (middle Miocene) of Panama and *C. staminata* (Dall, 1898) from the Chipola Formation (early Miocene) of Florida. *C. staminea* (Say; 11 831) is likely also related from the Pliocene of South Carolina.

Other species that have been assigned to *Cunearca* do not have the enlarged central ribs, but they do possess anterior ratchet sculpture. These include the eastern Pacific *C. nux* and *C. bifrons*. The early Miocene *C. staminata* likewise has ratchet sculpture and its central ribs are not enlarged. Woodring (1973) and del Río (1991, 1992) assigned species like this to *Potiarca* Iredale, 1939, a taxon based on *Potiarca (pilula) saccula* Iredale, 1939, a likely synonym of *P. pilulua* (Reeve, 1843). Lamprell and Healy (1998) apparently considered *Potiarca* a synonym of *Cunearca*, for they include *P. pilula* and related Indo-West Pacific species in *Cunearca*. These species are inequivalve and globose and in that sense resemble *Cunearca*, but there is no evidence of ratchet sculpture in these species. This implies that *Potiarca* should be considered a tropical Indo-West Pacific group distinct from the tropical American *Cunearca*. Unfortunately, Iredale (1939) did not compare his *Potiarca* with *Cunearca*. I consider *Cunearca* to consist of two groups, one based on *C. brasiliana*, and the other based on *C. nux* and *C. staminata*.

The tropical eastern Pacific *Anadara perlabiata* (Grant and Gale, 1931) does not have ratchet sculpture and is like most other anadarines in having imbricate periostracum on the shell's posterior sector. Despite its similarities in shell form to species of *Cunearca*, the absence of anterior ratcheting in *A. perlabiata* likely indicates that this species does not belong in *Cunearca*, where Olsson (1961) assigned it.

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Neptunea sakurai (Ozaki, 1958) (Gastropoda: Buccinidae) from middle to upper Pleistocene deposits in the southern part of the Japan Sea

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ABSTRACT

An extinct buccinid species, *Neptunea sakurai* (Ozaki, 1958), belonging to *N. lyrata* stock, was collected from the Middle to Upper Pleistocene deposits on the seabed at upper bathyal depths in the southern part of the Japan Sea. This is the first record of this species from the Middle to Upper Pleistocene deposits, and it indicates that this species survived the end-Early Pleistocene extinction event in the lower sublittoral to upper bathyal depth.

Additional Keywords: Marine, fossil, deep water, end-Early Pleistocene extinction event

INTRODUCTION

Pliocene to Quaternary molluscan fossils have rarely been recorded from outcrops on the seabed of the Japan sea. Many shallow-water species have been illustrated from the upper Pliocene to lower Pleistocene deposits off the western Honshu (San'in region) in the southern part of the Japan Sea (Okamoto, 1978; Okamoto and Honza, 1978). These assemblages indicate a mixture of the cold-water species dominant Omma-Manganji fauna (Otuka, 1939a) and the warm-water Kakegawa fauna (Otuka, 1939b). The molluscan fossils from the southern part of the Japan Sea are important for estimating environmental change because few marine deposits crop out in the western Honshu.

Several specimens of the fossil buccinid of the genus *Neptunea* collected in upper bathyal depths of the southern part of the Japan Sea were acquired from commercial bottom trawlers. This paper discusses the identify of this species and significance of the occurrence.

MATERIALS AND METHODS

Fossil specimens of a species of *Neptunea* were recovered from two closely situated localities in the southern part of the Japan Sea (Figure 1). Nine specimens from Loc. 1 (35°43′21″ N, 130°43′21″ E, 305m depth), and 14 specimens from Loc. 2 (35°29′30″ N, 130°44′40″ E, 201m depth), were examined for the present study.

Isotope ages were determined using two specimens from Loc. 1, and assigned to 47,565 ± 483 yrBP and 51,400 ± 680 yrBP by the Institute of Accelerator Analysis Ltd., based on ^{14}C methodology (Bronk Ramsey, 2009; Heaton et al., 2020). However, these ages seem to be near or slightly over the limit of this method, which is usually within the range of 50 ka to 60 ka (Trumbore, 2000). There is a possibility for the age to be older than late Pleistocene. The calcareous nannofossil assemblage attached to the present specimens may also be helpful to estimate the age; accordingly, six nannofossil species were identified from the relatively hard sediments scraped off from the inner side of apertural parts of *Neptunea* species from Loc. 1. Among them, the occurrence of a coccolithophore *Emiliania huxleyi* indicates the fossil's age to be from 265 ka (middle Pleistocene) to the present (Sato et al., 2009). From these data, the age of the fossils can be assigned to the middle to late Pleistocene.

Institutional Abbreviations: IGPS, Institute of Geology and Paleontology, Tohoku University, Sendai; NMNS PM, Paleontological molluscan collection of the National Museum of Nature and Science, Tokyo.

SYSTEMATICS

Family Buccinidae Rafinesque, 1815

Genus *Neptunea* Röding, 1798

Subgenus *Neptunea* Röding, 1798
Type Species: *Murex antiquus* Linnaeus, 1758 by subsequent designation (Sandberger, 1861).

Neptunea (Neptunea) sakurai (Ozaki, 1958)

(Figures 2–13)

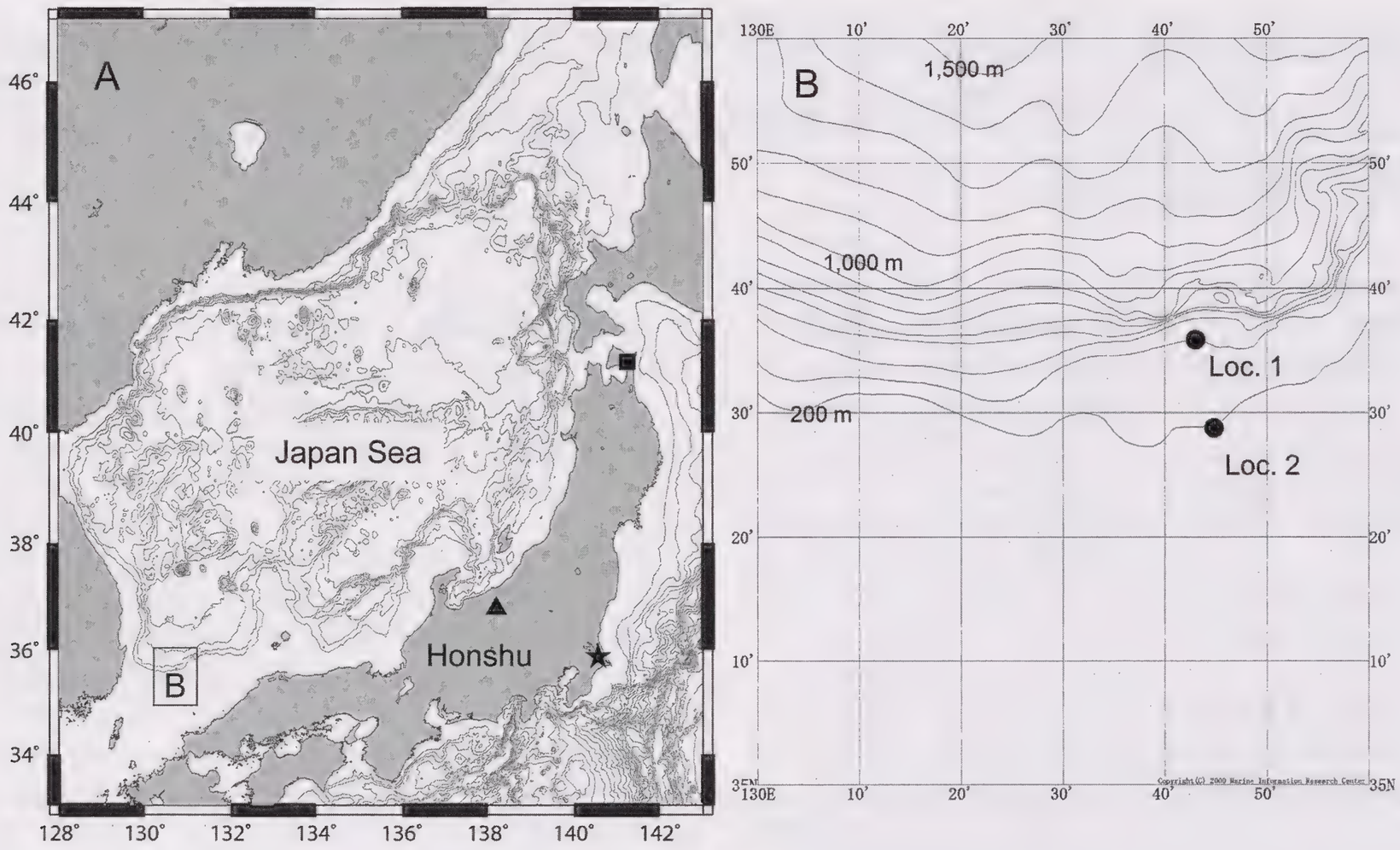


Figure 1. Localities of study fossils. A square area "B" shown in the map "A" (left) is enlarged in the right. Black circles indicate localities of the present material. A black star shows the type locality of *Neptunea sakurai* (Ozaki, 1958), a black square and a black triangle show additional localities, Hamada Formation in Aomori Prefecture, and Ogikubo Formation in Nagano Prefecture, respectively.

Suavodrillia sakurai Ozaki, 1958: p. 162, pl. 16, figs. 8, 9.
Neptunea sakurai (Ozaki) – Hatai et al., 1961: pl. 3, fig. 17; Masuda, 1982: pl.156, fig. 1455; Nagamori, 2014, pl. 18, figs. 8a, b.
Neptunea (*Neptunea*) *sakurai* (Ozaki) – Amano, 1997: figs. 3–4, 5; Shimaguchi and Nara, 2015: pl. 3, fig. 4.
not *Neptunea sakuraii* (Ozaki) – Baba, 1990: p. 164, pl. 10, fig. 19 [=? *N. lyrata* (Gmelin, 1791)].

Type Locality: Cliff, 500m south of Matsugishi railway Station, Choshi City, Chiba Prefecture, Pacific side of central Honshu. Lower Pleistocene Iioka Formation.

Type Material: Holotype, NMNS PM 4500 (Figures 5, 6).

Original Description: "Shell moderate in size, fusiform; although the early whorls are broken, spire apparently shorter than the apertural part, apical angle 60; each whorl sculptured by a strong, broad, rounded carina below the middle, the surface above it slightly convex, and concave below; body whorl with 11 primary cords below the carina, with secondary ones in the narrow interspaces; obsolete subsutural cord visible in front of suture. Entire surface covered with numerous distinct lines of growth, which intersect the carina and revolving cords thus giving rise to somewhat rugose appearance. Inner lip covered with narrow callus, outer lip strongly flexuous; canal moderately broad." (Ozaki, 1958, p. 162).

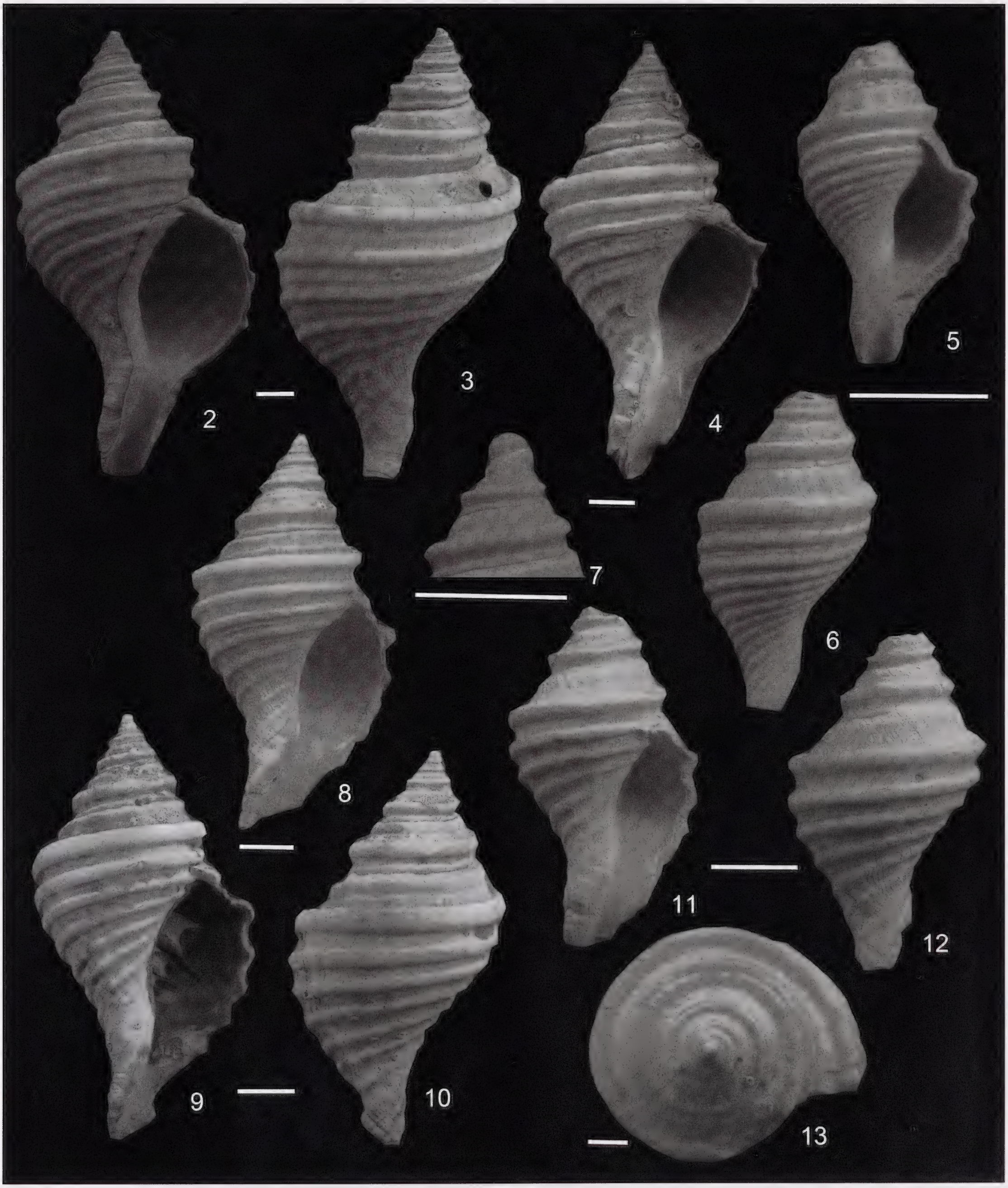
Description of the specimens from the southern part of Japan Sea: Shell medium in size for genus, up to 118.9 mm, moderately thick; protoconch (Figure 7) well preserved, smooth, consisting of two relatively large convex whorls (diameter = 3.0 to 3.3 mm); teleoconch of five and half whorls in largest specimens. Body whorl large, occupying about three-fourths of shell length. Suture deep. Penultimate whorl sculptured by three round-topped cords and fine growth lines; lower two cords strong, with middle one being most prominent, and uppermost cord situated below suture weakest with additional indistinct cord between middle and upper cords. Body whorl sculptured by eight to 12 round-topped cords (most frequently 10) with one interstitial weak cord and fine growth lines; strongest cord situated above periphery, producing rather convex shoulder; base ornamented with six to nine cords (most frequently eight); uppermost cord located just below deep suture. Aperture ovate; inner lip covered by thick calcareous callus; outer lip not thickened. Siphonal canal narrow, long and oblique. Fasciole narrow and relatively long.

Material Examined: Eight well-preserved specimens (NMNS PM 65148) from loc. 1, and 14 specimens (NMNS PM 65149) from Loc. 2 (Figure 1B).

Measurements: See Table 1.

Distribution: Pliocene; Ogikubo Formation in Nagano Prefecture (Nagamori, 2014). early Pleistocene; Iioka Formation in Chiba Prefecture (Ozaki, 1958) and Hamada Formation in Aomori Prefecture (Hatai et al., 1961; Amano, 1997; Shimaguchi and Nara, 2015). middle to late Pleistocene deposits from the western part of the Japan Sea (this study).

Remarks: Ozaki (1958) proposed this species in the turrid genus *Suavodrillia* Dall, 1918, based on single



Figures 2–13. *Neptunea sakurai*. **2, 3.** Specimen from Loc. 1, NMNS PM 65148-1. **2.** Apertural view. **3.** Dorsal view. **4.** Specimen from Loc. 2, NMNS PM 65149-3; Apertural view. **5, 6.** Holotype from the Iioka Formation, NMNS PM 4500. **5.** Apertural view; **6.** Dorsal view. **7, 8.** Specimen from Loc. 1, MNS PM 65148-4. **7.** Protoconch. **8.** Apertural view. **9, 10.** Specimen from Loc. 2, NMNS PM 65149-1. **9.** Apertural view; **10.** Dorsal view. **11, 12.** Specimen from the Hamada Formation, NMNS PM 58112; **11.** Apertural view. **12.** Dorsal view. **13.** Specimen from Loc. 1, MNS PM 65148-2, Apical view. Scale bar = 1cm.

Table 1. Measurements of specimens.

No.	NTW*	Height (mm)	Diameter(mm)	PSN**	BSN***
64148-1	5.5	117.2+	59.8	3	10
64148-2	5.5	109.8	60.9	3	10
64148-3	4	104.4+	62.7	3	11
64148-4	5	79.8	42.0	3	11
64148-5	5.5	118.9+	55.7	3	10
64148-6	4	104.0+	49.4	3	11
64148-7	4	80.8+	40.9	3	9
64148-8	4	93.1+	47.3	3	11
65149-1	5	75.1	37.9	3	9
65149-2	5.5	80.6	43.7	3	8
65149-3	5	87.6	44.1	3	9
65149-4	5	55.4+	33.0	3	10
65149-5	4	75.8+	42.1	3	9
65149-6	4	74.7+	41.4	3	8
65149-7	4.5	72.1+	39.0	3	10
65149-8	3	56.0+	34.2	3	9
65149-9	4	76.2+	39.4	3	9
65149-10	4	58.1	31.6	3	10
65149-11	4	82.1+	43.7	3	12
65149-12	5	68.1+	37.7	3	9
65149-13	4	64.9+	40.6	3	9
65149-14	5	85.1+	42.8	3	13

*NTW= number of teleoconch whorls; **PSN= number of spiral cords on the penultimate whorl; ***BSN= number of spiral cords on the body whorl. NMNS PM 64148 from Loc. 1 and NMNS PM 65149 from Loc. 2.

juvenile specimen (height = 22 mm) from the lower Pleistocene Iioka Formation in Chiba Prefecture on the Pacific side of central Honshu. The holotype has only one cord on the penultimate whorl and 12 cords on the body whorl. In describing the fauna from the lower Pleistocene Hamada Formation in Aomori Prefecture, Hatai et al. (1961) recorded this species and allocated it to the genus *Neptunea* Röding, 1798. When Amano (1997) illustrated immature specimens from the Hamada Formation stored at IGPS, he included *N. sakurai* in the *N. lyrata* stock as defined by Goryachev (1978). These specimens have one or three strong cords on the penultimate whorl and eight to 10 cords on the body whorl. Although these specimens are juvenile or immature shells, Shimaguchi and Nara (2015) illustrated for the first time a fully grown specimen, attaining about 100 mm in length, from the Hamada Formation. This specimen is most similar to our specimens from the southern part of the Japan Sea in having three spiral cords on the penultimate whorl and about 10 cords with one interstitial cord. Our specimens are therefore confidently identified as *Neptunea sakurai.*

According to the original description, the species was named after Dr. K. Sakurai. Thus, Masuda and Noda (1976) pointed out that the species name must be changed to *N. sakuraii* based on the Latin grammar. However, according to ICZN article 32.5, *N. sakurai* should be used regardless of its grammatical incorrectness, as it is the original spelling of the name.

This species is closely similar to the extant species, *N. excelsior* Fraussen and Terryn, 2017 recorded in the Eastern China, Korea, Primorie to central Sakhalin in the Japan Sea, Hokkaido, the Sea of Okhotsk, and the southern Bering Sea off Kamchatka. Both species share a similar number of strong spiral cords with at least one interstitial cord, not fine threads. However, *N. excelsior* differs from *N. sakurai* in having a larger shell (up to 190 mm), flat-topped cords sometimes with secondary fine cords on top and a shorter and wider siphonal canal. *Neptunea excelsior* has thus far not been recorded from the Japanese archipelago side of the Japan Sea.

Neptunea lyrata (Gmelin, 1791) is another related species, but it differs from *N. sakurai* by having a larger shell (attaining 187 mm in height) with a shorter siphonal canal and sculpture of many fine threads between strong spiral cords (Golikov, 1963; Fraussen and Terryn, 2017). Baba (1990: pl. 10, fig. 19) illustrated an incomplete specimen

of a species of *Neptunea* as *N. sakuraii* (*sic*) from its type locality, the Iioka Formation. However, the illustrated species has an angulated shoulder at the strongest cord on the body whorl and numerous fine interstitial threads. These characters agree with *N. lyrata*, not with *N. sakurai*.

DISCUSSION

In the Pliocene to Early Pleistocene, the Omma-Manganji fauna (Otuka, 1939a) flourished mainly in the Japan Sea borderland (Ogasawara, 1986; Amano, 2001, 2007).

The oldest specimen of *Neptunea sakurai* was recorded by Nagamori (2014) from the Pliocene Ogikubo Formation in Nagano Prefecture, near the Japan Sea side of central Honshu, together with some characteristic species of the Omma-Manganji fauna. Molluscan assemblages of the lower Pleistocene Hamada Formation in Aomori Prefecture include some characteristic species of the Omma-Manganji fauna, including *Neptunea sakurai* (Hatai et al., 1961; Ogasawara, 1977, 1986; Masuda and Ogasawara, 1981; Amano, 1997; Shimaguchi and Nara, 2015). In addition to the Hamada Formation, this species is also known from the lower Pleistocene Iioka Formation in Chiba Prefecture, central Honshu (Ozaki, 1958), based on the immature holotype. This species was considered to have become extinct due to end-early Pleistocene extinction events in the Japan Sea because of the environmental deterioration due to glaciation (Amano, 2004, 2007). Thus, the present finding of this species from the middle to upper Pleistocene deposits confirms its survival until a later time in the southern part of the Japan Sea. This is also the first record of this species from the seabed of the Japan Sea at upper bathyal depths (201 to 305m) at the present sea level.

Some deep-water molluscan species could successfully survive the end-early Pleistocene extinction as well as the Last Glacial Maximum (LGM) event. These include *Portlandia toyamaensis* (Kuroda, 1929), *Buccinum tsubai* Kuroda in Teramachi, 1933, and *B. striatissimum* Sowerby, 1899 (Amano, 1996, 2004, 2007). They might have survived in the depth range between 100 and 400m because the marine water with normal salinity and oxygen concentration (intermediate water) existed at this depth range during the glacial ages (Amano, 2004).

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